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REGENERATION OF *HETERODENDRUM* IN ARID SOUTH-EASTERN AUSTRALIA

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ABSTRACT: Work was carried out to see if the failure of *Heterodendrum oleifolium* to regenerate vegetatively and from seed in the arid zone is due to grazing, the physical environment, innate factors or some combination of these. Flowering and seed set were spasmodic in the study area. Insect predators destroyed up to 68 per cent of seed in the crowns. Many unattacked seeds were empty and the proportion of empty seeds appeared to increase with time from seed set. Enhanced germination after seed coat nicking demonstrated some hard-seededness.

Sucker shoots can arise from shallow, horizontal roots. Detached root pieces produced callus tissue but not suckers. Young plants readily produced stem suckers after decapitation. After root severance, callus swellings were common, but root suckering was rare. In the field, severance of roots by ploughing produced root suckers distal to the site of severance, suggesting control of suckering by the shoot apex. After wildfire, 19 per cent of mature trees were killed, mostly those smaller than 50 cm girth, while 30 per cent formed root suckers. At all sites, virtually all root suckering could be readily related to specific disturbance events and so was considered episodic.

Isoenzyme analysis to test genetic identity indicated that the frequently observed groves of *H. oleifolium* were clonal. Because suckering seems strongly dependent on disturbance, it is suggested that simply removing stock will not allow adequate regeneration. Management may need to provide sufficient fire frequency to initiate enough suckers for replacement of old stems and hence stand perpetuation.

A central problem for the management of arid zone vegetation in Australia is the partial or complete failure of some woody species to regenerate (Hall *et al.* 1964, Harrington *et al.* 1984), even though there is still controversy about how many species fall within this category (Stanley 1983, Chesterfield & Parsons 1985). *Heterodendrum oleifolium* (Sapindaceae), 'one of the most useful fodder trees in inland Australia' (Everist 1974), is a species which can fail to regenerate both in the presence of stock (Chesterfield & Parsons 1985) and, in at least some areas, in their absence (Sinclair 1984). The species is widespread in the Australian arid zone (see map in Hall *et al.* 1964). The aim of the present work is to test whether its regeneration both from seed and from root suckers is adequate in the study area and if not, whether grazing by stock is the sole cause of inadequate regeneration.

METHODS

Flower and Seed Biology

Flower, fruit and seed production was examined at a number of sites several times from February to December, 1985 (Fig. 1, Table 1, Appendix for locations). As diocey is common in the Family Sapindaceae, this was checked for as a possible aid in identification of clones (see later). All trees checked were monoecious. Seeds were classified as: (a) eaten by insects if seed coats showed characteristic signs of attack; (b) empty, if seed coats lacked such signs but were easily crushed between thumb and finger; or, (c) filled, if coats were filled with white, apparently live, tissue.

Seeds collected from trees between March and August, 1985 were surface sterilized (70% alcohol), variously treated (Table 2) and tested for germination for 6 weeks 20 per petri dish. It was not realized at the time that the seeds included both empty and filled ones. Germination trials were on Whatman grade 181 filter paper moistened with distilled water in a growth cabinet with 14 h/30°C light cycle and 10 h/15°C dark cycle [high temperature chosen following Burbidge (1960)]. A few trials used constant 26°C instead. The minimum number of replicates used was three (60 seeds).

A final trial, with seeds collected from Red Cliffs on 25 February 1986, used continuous light or continuous darkness at 25°C.

Suckering

Detached root pieces

In February, March, May and July, 20-30 cm lengths of lateral surface roots with diameters ranging from 2.5 to 27.5 mm (upper size limit determined by cutting capacity of secateurs) were collected, placed in a mixture of coarse sand, perlite, vermiculite and compost at a depth of 10 cm, put into a Melbourne glasshouse and examined for suckers after 10 weeks.

Seedling damage response

Eighteen month old seedlings were variously (a) decapitated just above soil level, (b) decapitated and treated twice weekly with 1% indole-3-acetic acid (IAA) in lanolin contained in Beem fixing capsules placed over the cut stem, (c) treated as for (b) but using lanolin alone, (d) had all roots severed at a 1 cm radius from the stem to a depth of 3-4 cm, (e) had all leaves removed and (f) left as controls. All plants were placed in a growth cabinet with a 14h/30°C day cycle and 10h/15°C night cycle for 10 weeks.

Fig. 1 – Location of the study sites.

Field observations

Suckering was examined at sites affected by fire, road grading, stock grazing and ploughing. Stem girth was measured 45 cm above ground level. Throughout the paper, the term 'tree' is used only where stems occur scattered singly and not where stems are clumped to form groves. To sample enough trees, Site 5a was combined with the closely-adjacent Site 5b (Appendix).

TABLE 2
EFFECT OF SEVEN TREATMENTS ON GERMINATION OF *Heterodendrum oleifolium* AFTER SIX WEEKS
(Data summed across collection dates and temperature regimes)

Treatment	Number of filled seeds	% germination
Control	80	12
Soaked 2h (water)	9	11
Leached 24h (running water)	21	19
Leached 48h (running water)	19	10
Soaked 24h (1N HCl)	43	17
Soaked 24h (10^{-4}M gibberellic acid)	10	10
Testa nicked*, soaked 24h (water)	37	35

* Nicking was always deep enough to expose white embryonic tissue.

CLONAL GROWTH HABIT

Site description and girth measurement

Heterodendrum oleifolium can occur naturally in clumps or groves. At Sites 3 and 8, scattered, natural *H. oleifolium* groves were the only woody species present, so that interspecific competition effects on possible clonal growth were minimal (Barnes 1966). Site 3 was grazed lightly by sheep; Site 8 had not been grazed by stock since 1975, but kangaroos, rabbits and some goats were present. For each grove, stem girths were measured as before. Some young root suckers at Site 8, all less than 30 cm high, were omitted as they seemed to have arisen from recent disturbance.

Isoenzyme analysis

Whereas seedlings should be genetically diverse, members of a clone should be identical in the absence of somatic mutation in root buds; isoenzyme analysis provided a convenient test of genetic identity (Sternberg

TABLE 1
Heterodendrum oleifolium SEED CHARACTERISTICS FROM FOUR SITES. PERCENTAGES GIVEN IN BRACKETS

Site	Source of sample	Collection date	Seed Numbers: Eaten by insects	Empty	Filled
7	Tree crowns	12 February 1985	n.d.*	55 (100)	0 (0)
12	Tree crowns	14 February 1985	n.d.*	85 (65)	46 (35)
12	Tree crowns	22 March 1985	n.d.*	457 (91)	43 (9)
12	Tree crowns	18 May 1985	460 (42)	574 (53)	57 (5)
12	Tree crowns	11 July 1985	221 (25)	637 (74)	8 (1)
11	Tree crowns	10 July 1985	98 (68)	37 (26)	8 (6)
2	Tree crowns	11 July 1985	39 (15)	209 (83)	4 (2)
12	Soil surface	18 May 1985	0	726 (99)	2 (1)
12	Soil surface	11 July 1985	0	235 (100)	0 (0)

* n.d. = insect damage present but amount not determined.

1976). Leaf samples from all stems within each grove were transported to the laboratory on ice, stored at 2°C, and samples (0.5 g) cut up and ground to powder in liquid nitrogen before adding grinding buffer, grinding to paste and the extract clarified by centrifugation. The grinding buffer was that used for buds by Cheliak and Pitel (1984) with the addition of 2.5 mM DIECA, 2 mM sodium metabisulphite and 2mM sodium tetraborate. The liquid extract was either placed in wells in the gel or absorbed onto filter paper wicks (Whatman 3 mm chromatography paper).

After various trials, the best starch-gel electrophoresis system proved to be 12.5% starch gel containing 0.005 M histidine pH8 gel buffer run with a 0.41 M sodium citrate pH 8 tray buffer. Gels ran for 4 h at 65 mA. Four enzyme systems were examined with the stains used by Fripp (1982).

As well as leaves from the two groves, leaves from various 18 month old seedlings (Forests Commission of Victoria nursery, unknown provenance) were also analyzed to try to encompass material with a wider genetic range.

RESULTS AND DISCUSSION

Flower and Seed Biology

In February 1985, fertile trees carried mature fruit and not flowers, reflecting the normal, predominantly late spring-early summer flowering time (see also Cunningham *et al.* 1981). Percentage of trees per site flowering and fruiting in the 1984-1985 season varied from 3 at Site 11 to 39 at 12 . While some seed was produced in the region in 1984, 1985 and 1986, there was none for several years before that (J.H. Browne & N.G. Aloizos pers. comm., Chesterfield & Parsons 1985), reflecting a widespread tendency for erratic flowering and/or seed set (Burbidge 1960, Hall *et al.* 1964).

The fruits range in size from 5-15 mm diameter and are of one to four locules. Mature seeds (5 mm diameter) are non-endospermic, globose, shiny, black and partly encircled by orange-red arils (Fig. 2). Seed crop data (Table 1) showed that insect larvae (superfamily Pyraloidea, T. New pers. comm.) destroyed up to 68 per cent of seeds present in the crown at any one time. Insect damage occurred at least from February onwards, although it was not quantified until May. The larvae were never found in fruits or seeds beneath the trees (Table 1).

For seeds unaffected by insects, the per cent filled was highly variable and often low (Table 1). While the initial figures could reflect factors like pollen sterility (Haegi & Barker 1985) and parthenocarpy (Gustafson 1942), the data for Site 12 also suggest declining percentages of filled seeds from February to July. This reduction could involve factors like insect-introduced fungal diseases (as in *Pistacia*, Jaynes 1979), seeds being innately short-lived (Mayer & Poljakoff-Mayber 1982), drying or heating effects on viability or even selective removal of filled seeds from crowns by birds or insects. Very few filled seeds were found on the soil surface (Table 1); it is not known whether removal of filled seeds by ants contributes to this. By July, filled seeds were scarce both on the soil surface and in the crowns. However, some trees were exceptional; at Nowingi as late as 19 August 1985, amongst many *Heterodendrum* trees lacking seed, a single tree was found carrying a large seed crop. Of the seeds unattacked by insects, 20% were filled.

Some preliminary work suggests that, in the crown, the arillate seeds in open fruits were much more likely to be filled than seeds from undehisced fruits at any given time.

When the germination experiments were set up, the low percentage of filled seeds had not been recognized. Filled seeds were so few that the results are preliminary only and statistically unanalyzable. Those presented (Table 2) are summed across collection dates and the two temperature regimes, as these had no apparent effect. Seed nicking appeared to enhance germination (Table 2), suggesting that some seeds had an impermeable testa as is known for other species in this family (Floyd 1966). The germination of a few untreated seeds (Table 2) suggests that some 'soft' seeds are present in seed batches less than one year old. Germination is epigeal.

The 1986 seed sample had a high percentage of seeds held in very recently-opened fruits. It showed that high germinability is possible with scarified fresh seed and confirmed the occurrence of hard-seededness (Table 3).

It is clear that problems of spasmodic flowering, seed emptiness, seed predation by insects and low germinability occur. The spasmodic flowering and apparent rapid decline in seed viability with time strikingly resemble the behaviour of *Acacia harpophylla*, another root-suckering species (Johnson 1964).

Suckering

Transverse sections showed that the horizontal, subsurface organs from which suckers often arise are in fact roots.

Detached root pieces

No root suckers formed on any of the detached root pieces. Swellings of callus tissue on both damaged and undamaged surfaces occurred on some pieces of 3 to 21 mm diameter. It is not known if these were precursors to roots or shoots. Some pieces produced young roots which did not arise from swellings. In *Populus*, root suckers may occur in as little as two weeks but are common within seven weeks from excision (Farmer 1962, Schier 1972).

Seedling damage response

After 10 weeks, the decapitated plants had produced sucker shoots from the cut section. Those decapitated then treated with IAA and lanolin gave no response but neither did 7 out of 10 of those given only lanolin, possibly because IAA and lanolin were added by pouring into Beem fixing capsules fitted over the stumps. The capsules may have prevented stem suckers from developing. Root severance produced swellings of callus

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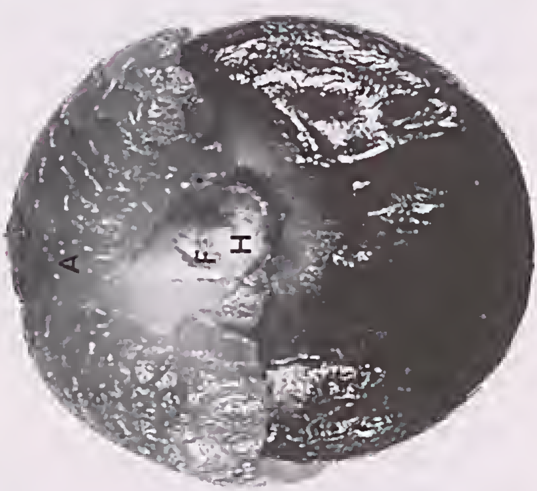

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Fig. 2—Mature seed of *Heterodendrum oleifolium* partly enclosed by aril (A), showing the funicle (F) and the hilum (H). × 2.4.

Fig. 3—Adult stems of *Heterodendrum oleifolium* (upper left) and road verge at Site 5 showing edge of grader scrape (G) and line of *H. oleifolium* root suckers to 1 m high (S) within scraped area. Note absence of suckers in undisturbed area to left of scrape.

Fig. 4—Adult stems of *Heterodendrum oleifolium* 6 m high with exposed lateral roots 15 m long bearing suckers. Former stock holding paddock, Site 8.

Fig. 5—*Heterodendrum oleifolium* suckering after 1975 fire, Site 6. Arrowed from right to left are (a) adult parent trunk and crown killed by the fire (b) grazed sucker 90 cm high 3.5 m from trunk and (c) ungrazed sucker 1.7 m high 8.2 m from trunk. (a), (b) and (c) are in a line and are very likely to be part of one individual. Live tree in centre is *Casuarina cristata*.

TABLE 3
EFFECT OF THREE TREATMENTS ON PERCENTAGE GERMINATION OF 1986 *Heterodendrum oleifolium* SEED AT 25°C.
All values based on 100 filled seeds per treatment

Treatment	Time	
	7 days	19 days*
Control	8	19
Nicked, continuous light	38	88
Nicked, continuous darkness	82	93

* All germination had ceased after about 30 days.

tissue on both attached and detached roots, some initiation of new roots and also, a single root sucker distal to the point of severance. The sole response to leaf removal was rapid growth and leaf production by axillary buds.

Taken overall, the results show considerable resilience to severe damage in 18 month old seedlings. The responses to decapitation and defoliation are consistent with views that these treatments reduce the flow of auxin and remove the inhibition to preformed dormant buds (Farmer 1962, Eliasson 1969). In the present case, it is usually dormant stem buds that become active; these may re-establish apical dominance thus preventing any development of root buds and hence of root suckers.

Field observations

Despite detailed search, no root suckers were found at any undisturbed site. Excavation showed that suckers usually arose from lateral roots from 2 to 15 cm deep. Where roots were severed by ploughing, all resulting suckers developed only on the severed root but not necessarily close to the point of severance (Table 4). All suckers produced after road grading were in the graded area clear of the undisturbed area (Fig. 3), suggesting the same effect. Such distal sucker production also occurs in *Populus tremuloides* and *Liquidambar*

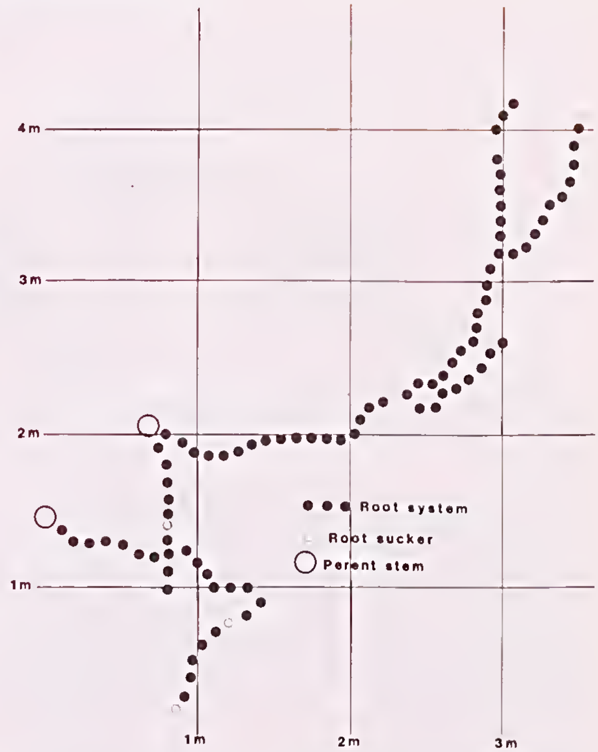

Fig. 6—Plan diagram of suckering *Heterodendrum oleifolium* root systems, Site 6.

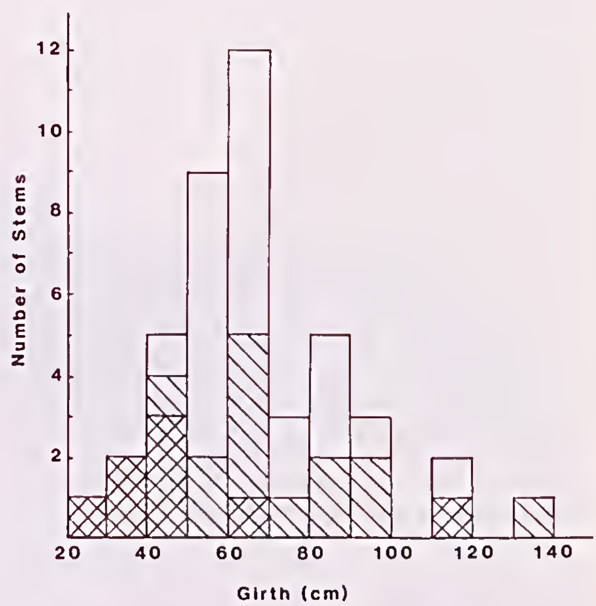

Fig. 7—Girth histogram for *Heterodendrum oleifolium* at Site 6 showing responses to the 1975 wildfire. Cross-hatching shows trees killed by fire, diagonal hatching shows trees producing root suckers after fire, no hatching shows live trees without root suckers.

TABLE 4
RELATIONSHIP OF DISTURBANCE TO ROOT SUCKERING IN *Heterodendrum oleifolium*

Site	History	Number of root suckers per adult stem*	Observations
1	Ploughing	26	Suckers distal to site of root severance
5	Road grading	21	Not excavated. See text
8	Stock holding yard	0.2	Suckers arising from damaged roots exposed by erosion
6	Wildfire 1975	1	Suckers present on undamaged roots
10	Wildfire 1984	0.5	Suckers present on undamaged roots

*Mean values. Sample size from three to 699.

styraciflua and suggests that root suckering is controlled by the shoot apex (Farmer 1962, Kormanik & Brown 1967).

At site 8, exposed lateral roots 15 m long were attached to adult stems 6 m high (Fig. 4). Topsoil erosion here probably followed overstocking. Suckers occurred both on broken and unbroken roots. It is not known if the latter had been damaged (e.g. by hoofs). Site 6, is thought to have been burnt by a high intensity wildfire in 1975. Nineteen per cent of mature *Heterodendrum* trees were killed outright, mostly smaller trees of less than 50 cm girth (Fig. 7). It seems very likely that root suckering sometimes occurred on plants whose main stem was killed by fire (Fig. 5) but more usually on plants whose main shoot system eventually recovered and produced a new crown. The root suckers were up to 8.2 m from the parent stem (Fig. 5). Thirty per cent, in a range of sizes, formed root suckers, while 51 per cent either showed no obvious damage 10 years later or had a few epicormic shoots usually at the base of the trunk. At this site, excavation around mature, burnt stems of *Heterodendrum oleifolium*, revealed surface roots with suckers more than 3 m from the parent stem and showed how closely adjacent suckers can arise from different parent stems on intersecting roots (Fig. 6). Although these suckers are now approximately 10 years old, their average height is only about 30 cm. Examination suggests that this is caused by stock grazing. The only large sucker found was 1.7 m high (Fig. 5) and was flowering for the first time. Little is known of normal rates of height growth.

Finally, site 10 had been burnt by wildfire in December 1984. Burnt *Heterodendrum* had not regenerated by August 1985 (possibly hindered by low rainfall) but some had done so by December of that year. Strikingly, the fire completely destroyed all aerial plant parts over large areas of mallee vegetation, but rapidly went out once it reached the different fuel conditions of the *Casuarina cristata-Heterodendrum oleifolium* woodland, where it damaged only a few marginal trees. Only 12 such *H. oleifolium* trees could be found along a fire boundary of at least 6-7 km. Of these, five appeared to have been killed outright and four had epicormic shoots in the crown and/or the main trunk but lacked root suckers. Of the three with root suckers, two had totally dead main trunks.

There was no evidence of continuous variation in sucker size or age at any site. All root suckering seen initially could be readily related to specific disturbance events and so was considered episodic. The only records of *Heterodendrum* root suckering without obvious disturbance are those of Hall *et al.* (1964) and of Chesterfield and Parsons (1985) at their Site 5. While re-examination of the latter indicated no obvious disturbance, possibly past defoliation by drought, insects etc. could provide the stimulus for sucker initiation. There is a range of views on the role of disturbance in root suckering in other species. For example, in *Populus*, Farmer (1962) stressed the importance of removing inhibition by the shoot apex before root suckering will begin, while Barnes (1966) and Cook (1983) strongly implied that *Populus* clones can develop gradually by suckering of a continually expanding root system without any damage to shoots or roots. Moar (1955) stressed that *Dacrydium colensoi* in New Zealand will root sucker without disturbance and treated this as the accessory type of suckering (part of normal development) compared to the reparative type (sequel to root injury or shoot destruction).

CLONAL GROWTH HABIT

Girth measurement

At both sites, stems of *Heterodendrum oleifolium* of less than 20 cm girth were absent (Figs. 8 & 9) other than some small root suckers at Site 8. Both histograms may represent single normal distributions as could be caused by a single suckering episode. The larger girths at Site 3 could relate to some combination of site conditions, lower stem density or greater age. There were no signs of large, old, possibly parental stems or stumps in the middle of or near the groves.

Maximum grove diameters at Sites 3 and 8 were 28 m (17 stems) and 18 m (28 stems) respectively (Fig. 9).

Isoenzyme analysis

All samples showed the same two-banded pattern for the glucosephosphate isomerase system. For the other enzyme systems, while each grove was invariant, Sites 3 and 8 were completely different. Further variability was seen in the seedlings (Fig. 10). Such invariance within groves combined with clear isozyme differences from other provenances strongly suggests a clonal origin for

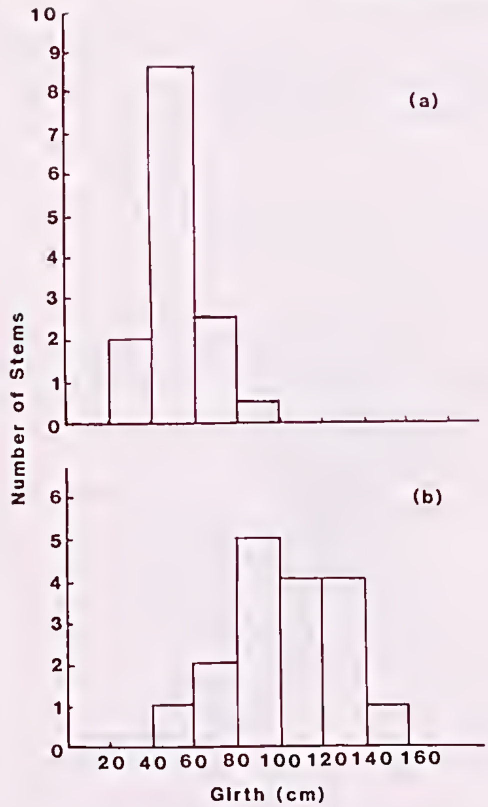

Fig. 8—Girth histograms for groves of *Heterodendrum oleifolium*. (a) At Site 3. (b) At Site 8.

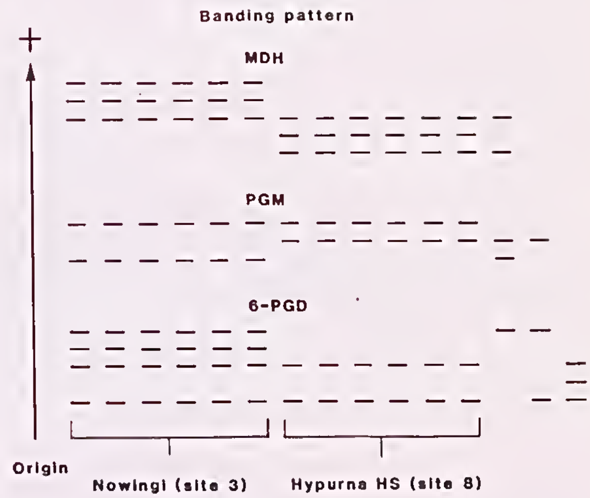

Fig. 10—Representative zymograms for three enzyme systems for six mature stems at Site 3, six at Site 8 and three seedlings. Every banding pattern shown was found in at least one seedling. MDH = malate dehydrogenase, PGM = phosphoglucomutase, 6-PGD = phosphogluconate dehydrogenase.

Fig. 9—The analyzed *Heterodendrum oleifolium* grove 6 m high and 28 m across at Site 3. Note browse line maintained by sheep at about 75 cm above ground.

the groves (Sternberg 1976, Huenneke 1985), supporting previous suggestions to that effect (Hall *et al.* 1964, Beadle 1981). While maximum clone size documented was 28 m diameter, analyses are needed over larger areas. For example, at Site 8, large patches of *Heterodendrum oleifolium* very close to the grove analyzed could possibly all have constituted a single clone at least twice that size. In *Populus tremuloides*, clone size can reach 47,000 stems over 43 ha (Cook 1983).

Clonal growth may be significant in semi-arid and arid areas because it minimizes the necessity for seedling establishment and may, by continuous rejuvenation, increase longevity up to the point of virtual or absolute immortality (Muller 1951, Noble 1986). In the present work, it was not possible to find senescing mature stems to see if senescence can initiate sucker formation. Immortality or even great longevity should not be assumed under present conditions given widespread death of old stems of *Heterodendrum* without replacement at Koonamore (Hall *et al.* 1964, Sinclair 1984). Potentially, death of mature stems could be accompanied by cessation of suckering and death of root systems.

The present girth data are consistent with the idea of root suckering and clonal growth being caused by episodic events of which fire may be the most likely.

CONCLUDING DISCUSSION

Overall, the data suggest that flowering and seed characteristics of *Heterodendrum oleifolium* make seedling establishment difficult and therefore rare. The species could often survive damage by fire and other agencies by producing root suckers and epicormic shoots.

The present work is consistent with previous findings that *H. oleifolium* will not regenerate adequately from suckers where stock are present (Chesterfield & Parsons 1985). However, the recommendation that simply spelling from stock will allow regeneration from suckers (Chesterfield & Parsons 1985) may need modifying. *H. oleifolium* may be so strongly dependent on damage by fire or other agencies for the initiation of suckering and clonal growth that just removing stock will not be sufficient. It is thus important to know the fire frequency required to permit replacement of stems by new suckers, since the intervals between fires may exceed 50 years (Hodgkinson & Harrington 1985). Management of *Heterodendrum* populations may therefore require not only control of mammal browsing but also the regular incidence of a disturbance agent like fire may be needed to ensure sucker initiation, sucker protection and stand perpetuation.

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APPENDIX

LOCATION OF STUDY SITES

Site no.	Grid reference*	Details
1	XG 080 710	Nowingi, tree in recently ploughed paddock
2	XG 072 708	Nowingi, grazed by stock, otherwise undisturbed
3	XG 005 704	Nowingi, grazed by stock, otherwise undisturbed
4	WG 355 935	Yarrara, undisturbed
5a	WG 356 933	Yarrara, cleared by road grader
5b	WG 401 924	Yarrara, cleared by road grader
6	XH 246 217	Trentham Cliffs, burnt by 1975 wildfire
7	XH 302 257	Montarna, undisturbed
8	393 853	Hypurna, former stock holding yard
9	386 857	Hypurna, undisturbed
10	359 879	Canopus, burnt by 1984 wildfire
11	142° 52′ north-33° 52′ east	Murragai, trees in recently ploughed paddock
12	XG 105 820	Castle's Crossing Bushland Reserve, undisturbed

* Grid references from 1:100,000 topographic maps except for sites 8-10 (1:250,000) and 11 (1:1,000,000)